Lethal coupling

It has been well recorded in a number of species of insects and spiders that males appear to allow themselves to be killed and eaten by a female after mating. For one spider it has been recently demonstrated that this sacrifice represents a reproductive investment on the part of the male. But new work by Matthias Foelmer and Daphne Fairbairn at Concordia University, Montreal and the University of California, Riverside, reported in the Proceedings B of the Royal Society, London (published online) offers the first evidence that males of one species of spider undergo programmed death immediately following mating and consider the potential adaptive significance of such an unusual behaviour.

The two researchers have been studying a species in the cannibalistic genus of orb-weaving spider, Argiope, where there has been some suggestion males may die after mating. But now the researchers have provided evidence for this.

Mating is a complex business for these spiders. The pedipalps, the pair of extremities posterior to the fangs, are morphologically derived to function as copulatory organs. Each palp inserts into one of the female's paired genital openings, which lead to separate sperm storage organs. On insertion, the distal bulb of the palp is inflated through increase in haemolymph pressure, which leads to the coupling of the palp with the female's genital plate. In the species studied, *A. aurantia*, males pursue two alternative mating strategies: if they encounter a juvenile female, one moult away from adulthood, they may cohabit with her on her web. They then try the two-stage

Death by design: Could the males of the orb-weaving spider, Argiope aurantia, be programmed to die immediately after copulation? New research suggests that they can. (Phototgraph: Oxford Scientific Films)

copulation while she in moulting and is unable to attack. However, if a male encounters a mature female, he may court her and if the female accepts, the male inserts the first palp. He then has to withdraw, re-court and insert the second palp. But in this situation the female can attack at any time.

The researchers therefore looked at the fate of males under both mating strategies in natural populations, in caged studies in the field and in laboratory experiments. They found that all males that managed two insertions with moulting females, in spite of their lack of defences, died while still in copulatory position. During staged matings with mature females, all males vigorously tried to escape from the female by jumping off her body after a very short insertion of the first palp. However, all males became motionless and assumed the typically dead posture after insertion of the second palp. The dead male was eventually pulled out by the female. In spite of the different outcome, males underwent the same level of attack from females both at the first and second insertion, the researchers observed. They also removed some males immediately after they had inserted the second palp, before the female could attack, but these all rapidly died too.

The authors consider what evolutionary advantage this strategy may confer. They note that, in natural populations, about 60 per cent of females are mated while moulting. Males fight for access to moulting females, but death during copulation with a palp inserted makes them much harder to remove from the female and they therefore may act as whole-body mating plugs, making it more difficult for other males to gain access to the female during her moult.

Primer

Lineage compartments in *Drosophila*

Seth S. Blair

Like many other tissues, the appendages and body wall of adult *Drosophila* are patterned during a period of intense cell proliferation. The ectoderm in the head and thorax of adult *Drosophila* is formed from epithelial invaginations, termed imaginal discs, that are set aside during embryonic development. During the three larval instars each disc grows from tens to tens of thousands of cells. Proliferation is not spatially restricted, and the cell lineages that form specific tissues within the epithelia of the appendages are largely random. Many tissue-specific decisions and cell lineages are not fixed until just prior to overt differentiation of the respective tissues. Thus, most ectodermal cells remain pluripotent until quite late in development, and cell-cell interactions play a critical role in the final choice between alternative fates.

The 'compartmental' lineage restrictions are, however, striking exceptions to this rule. As first defined by Garcia-Bellido and his co-workers, compartments are domains between which cells cannot mix. The progeny of single cells in imaginal discs, commonly marked using mitotic recombination, normally form coherent 'clones' (Figure 1). While cell migration and intermixing with neighboring cells is limited, clone boundaries are normally irregular and non-stereotyped. At compartmental boundaries, however, clones end at fixed anatomical positions and do not intermingle with cells of the other compartment.

In a sense, the lineage compartments of *Drosophila* epithelia are an extreme form of a very common theme in developing

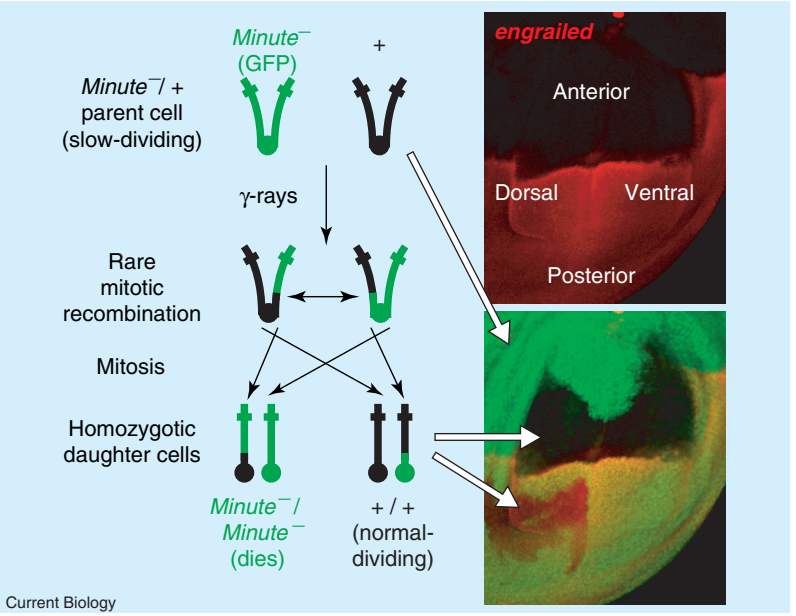

Figure 1. An example of using mitotic recombination and the *Minute* mutation to identify lineage compartments in the developing wing imaginal disc. Mitotic recombination between a GFP-tagged (green) *Minute* mutant (*ubi-GFP M(1)o*^{sp}) and a wild-type chromosome arm is induced with γ-rays early in larval development to create non GFP-expressing wild-type cells growing in a *Minute*/+ wing disc (green cells in photograph). The wild-type cells have a growth advantage over their slow-dividing *Minute*/+ neighbors. The right panels show the prospective wing blade portion of the wing imaginal disc at late third instar, just prior to metamorphosis. An anterior wild-type cell has divided to produce an unlabeled clone following a portion of the A/P compartment boundary, as defined by the strong expression of the selector gene *engrailed* (red). A posterior and dorsal cell have divided to produce a clone following part of the D/V compartment boundary.